Redescription of *Eurycephalochelys*, a trionychid turtle from the Lower Eocene of England

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Synopsis

Since Moody & Walker first described *Eurycephalochelys fowleri* in 1970, two more skulls have been discovered in the Bracklesham Series (Lower Eocene) of Sussex. These specimens, while supporting the original description of the species and validating the restoration attempted in the earlier publication, also provide further data on its morphology, size and stratigraphical range. A re-diagnosis is given.

Introduction

Continued collecting from the shoreline deposits of Bracklesham Bay at East Wittering by Mr R. Fowler has yielded several testudinate specimens. Amongst these are limbs and shells of both podocnemid and trionychid turtles and two skulls referable to *Eurycephalochelys fowleri*; Mr Fowler, who also discovered the holotype, has presented these skulls to the Department of Palaeontology, British Museum (Natural History). The first (R8694), virtually complete, was found in an oyster bed within the Cakeham Beds (Curry *et al.* 1977), whilst the second (R8695), represented only by the bones of the ventral or palatal surface, was found in the Nipa Bed at the base of the Cakeham Beds (Figs 1, 2).

The discovery of the two specimens, particularly R8695, confirms the existence in Cuisian times of a trionychid far larger than any other described species, fossil or extant. The two skulls show most of the characters described in 1970 by Moody & Walker.

Description

Order **TESTUDINES**

Suborder **CRYPTODIRA**

Superfamily **TRIONYCHOIDEA** Fitzinger 1826

Family **TRIONYCHIDAE** Fitzinger 1826

Genus ***EURYCEPHALOCHELYS*** Moody & Walker 1970

Type species. *Eurycephalochelys fowleri* Moody & Walker 1970.

Emended diagnosis. Quadrate condyle situated relatively far back, so that it lies behind stapedial foramen, in line with opening of foramen magnum, with posterior edge in line with maximum width of basioccipital; occipital condyle projecting some distance behind it; inclination of forwardly-directed flange of quadrate more horizontal than in other trionychids. Canalis alveolaris superior (internal maxillary foramen) situated at base of

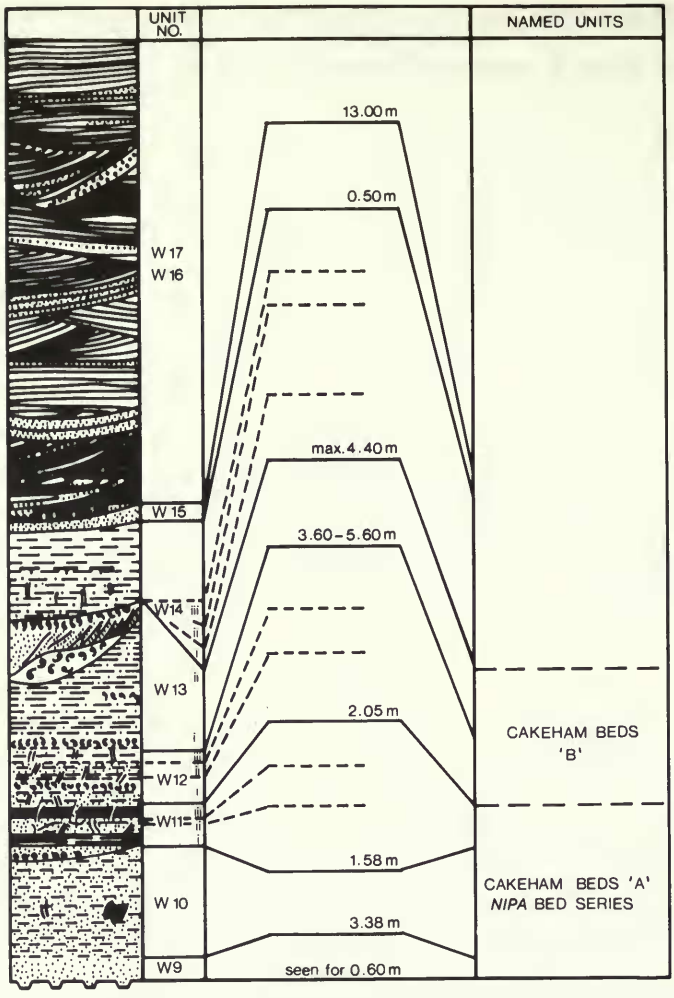

Fig. 1 Upper part of the Wittering Division stratigraphy (after Curry *et al.*, 1977).

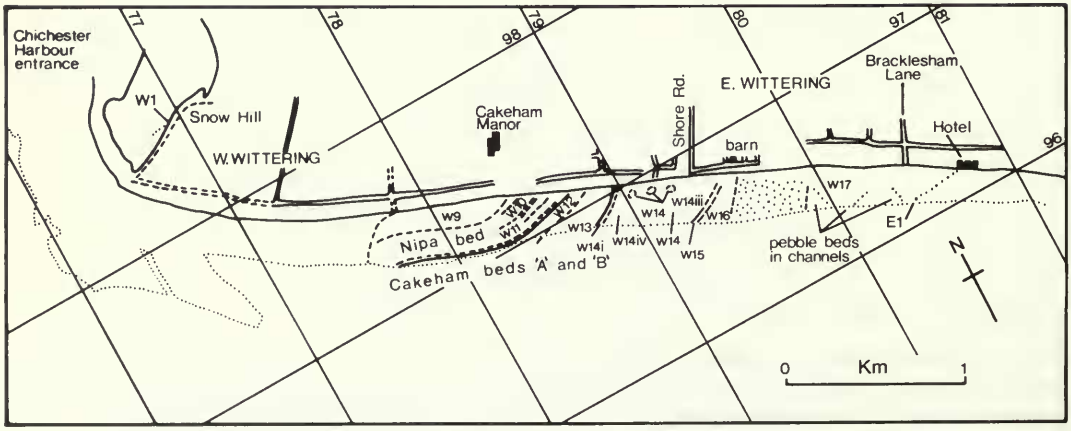

Fig. 2 Map of Wittering foreshore exposures, to show the site of the Cakeham Beds (after Curry *et al.*, 1977).

vertically rising wall of maxilla. Anterior opening of foramen palatinum posterius situated to side of ascending process of palatine and not enclosed in base of that bone as in *Cyclanorbis*. Jugal bar originates well below lowest point of orbital margin. Foramen magnum, and brain cavity immediately anterior to it, rounded. Snout region short and broad, with distance from tip of premaxilla to front of orbit much greater than anteroposterior diameter of orbit. Maximum width of skull across jugal bars equal to width across articular region of quadrates. Maxilla very deep, being two-thirds as deep as vertical diameter of orbit. Orbits small, somewhat longer than high and directed upwards and slightly forwards. Area of quadrate exposed on dorsal surface not larger than area of prootic but of approximately equal size. Tympanic cavity shallow and triangular in outline. Walls of choanal vault very steep and well-rounded.

Eurycephalochelys fowleri Moody & Walker 1970

Holotype. Incomplete skull without lower jaw (R8445).

Referred specimens. An almost complete skull without lower jaw (R8694; Figs 3–5), and the palatal region of a very large skull (R8695). Casts of these specimens are in the collection of Mr R. Fowler, Moschatel, Church Road, East Wittering, Sussex.

Occurrence. The Wittering Formation, Bracklesham Series, Cuisian (Lower Eocene); foreshore, East Wittering, Sussex, England.

Description of new material. Of the two new specimens R8694 is exceedingly well preserved and, apart from some dorsoventral crushing of the prefrontal region, is almost perfect. It exhibits a profile closely resembling that of the original reconstruction (Moody & Walker 1970: 508) although some detailed differences can be observed. In dorsal view (Fig. 3) it can be seen that the width of the interorbital bar, at its narrowest point, is greater than the maximum dorsoventral measurement of the orbit. Further, the jugal bar is more curved than that depicted in the original reconstruction, and therefore enhances the overall broad appearance of the skull. Within the orbits the canalis alveolaris superior (internal maxillary foramen) is unquestionably situated in the floor of the orbit whereas that of the holotype is positioned in the medial wall of the maxilla. However, the foramen is still sited in a more lateral position than any known trionychid. The difference could be explained by either erosion of the holotype or by individual variation. The lateral surface of the parietal is more steeply inclined in R8694, and the parietal/supraoccipital spine, absent in the holotype, is more massive than that of most recent forms and lacks the sharp undercut edge they possess. It is unfortunate that the sutures in this skull are almost completely closed, for it makes it impossible to confirm that there is no sutural contact between the prootic and the opisthotic on the dorsal surface, nor is it possible to make any further comments on the relative size of the prootic and quadrate in that view.

In lateral view (Fig. 4) the skull shows the same steep facial angle, and with a complete interorbital bar it can now be said that the depth of the maxilla is much greater than the vertical diameter of the orbit. As the jugal bar is present it is seen to be very narrow dorsoventrally, being approximately one-third of the depth of the maxilla below the orbit. The stapedial foramen of R8694 does not form such an obtuse angle with the condyle of the quadrate as in the type specimen, nor does the forwardly-directed flange of the quadrate lie so close to the horizontal.

The palatal surface of R8694 (Fig. 5) is by far the most complete known and shows that the intermaxillary foramen was of moderate size and approximately the same length as the intermaxillary suture. The morphology of the choanal vault area appears to indicate a condition similar to that found in *Cyclanorbis*, in that the vomer would not have overlain the palatines to any degree and in consequence did not produce the strong central vomerial ridge characteristic of *Trionyx*. The region differs from that of the reconstruction in that the anterior margins of the choanae are placed more posteriorly than in most trionychid genera

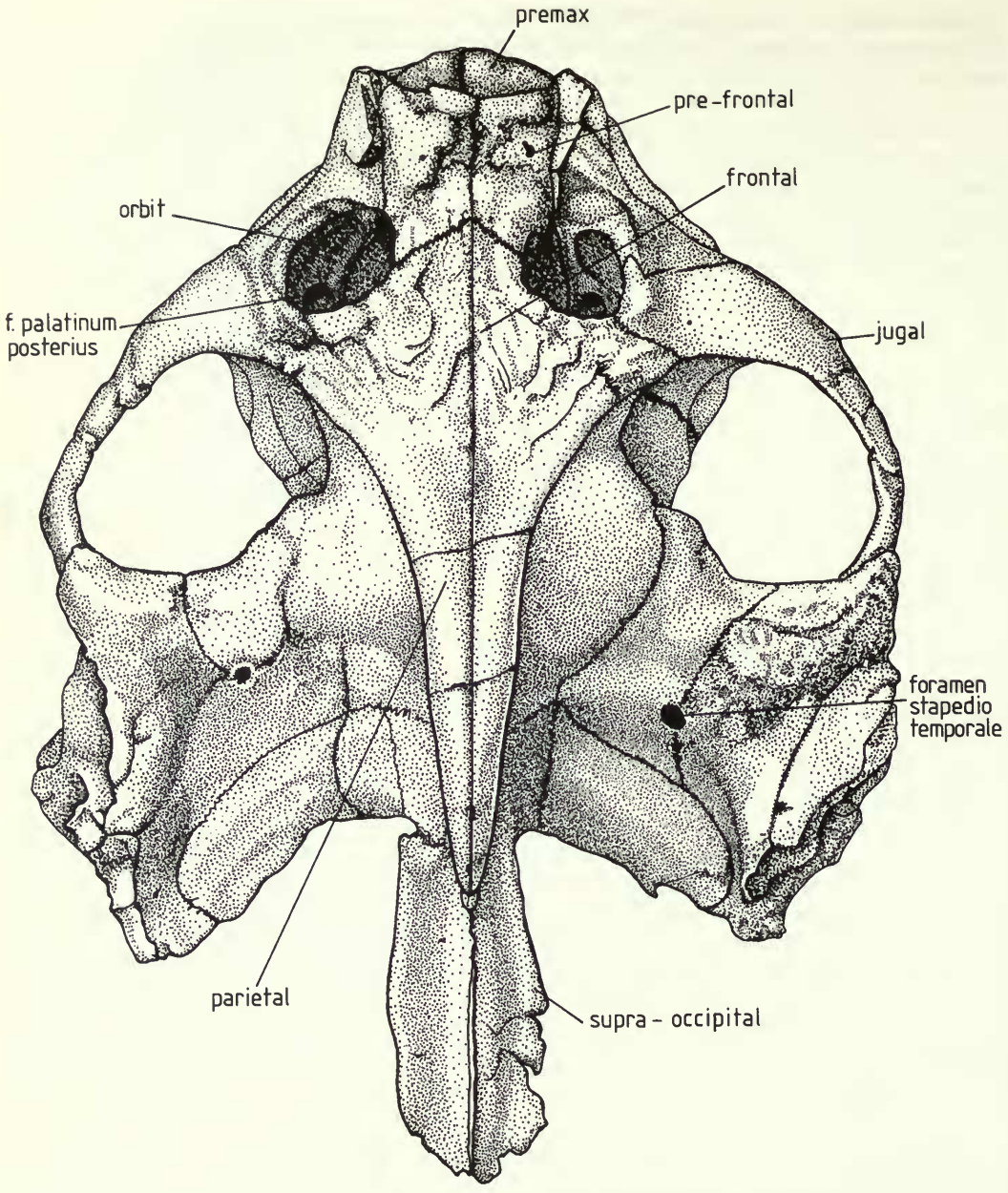

Fig. 3 *Eurycephalochelys fowleri* Moody & Walker, R8694. Dorsal view of skull, × 0·75.

and probably represent the primitive condition. In contrast the foramen palatinum posterius is in the normal position connecting internally, via a short canal, with an anterior foramen sited to the side of the ascending process of the palatine. This condition is more typical of *Trionyx* and *Cycloderma* than of *Cyclanorbis*, in which the internal formen occurs at the base of the process. The posterior openings of the foramen posterior canalis carotici interni are not visible in this view. The foramen is covered by the pterygoid and in this respect is similar to *Chitra*. In the original restoration, it was shown in the normal position and was therefore incorrectly placed.

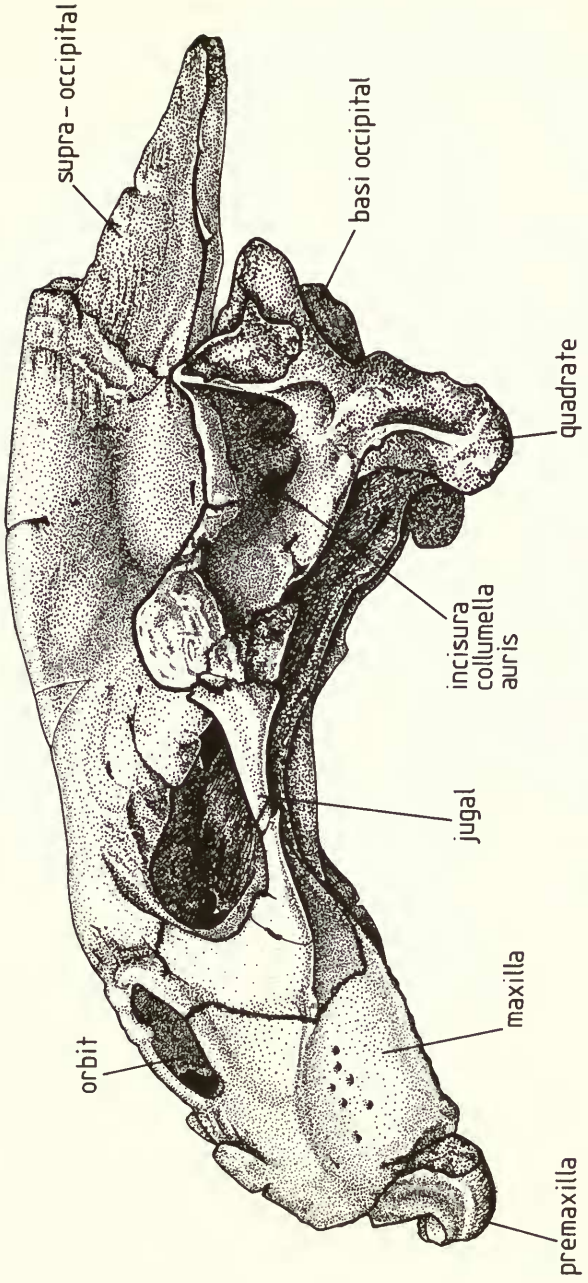

Fig. 4 *Eurycephalochelys fowleri* Moody & Walker, R8694. Left lateral view of skull, × 0·75.

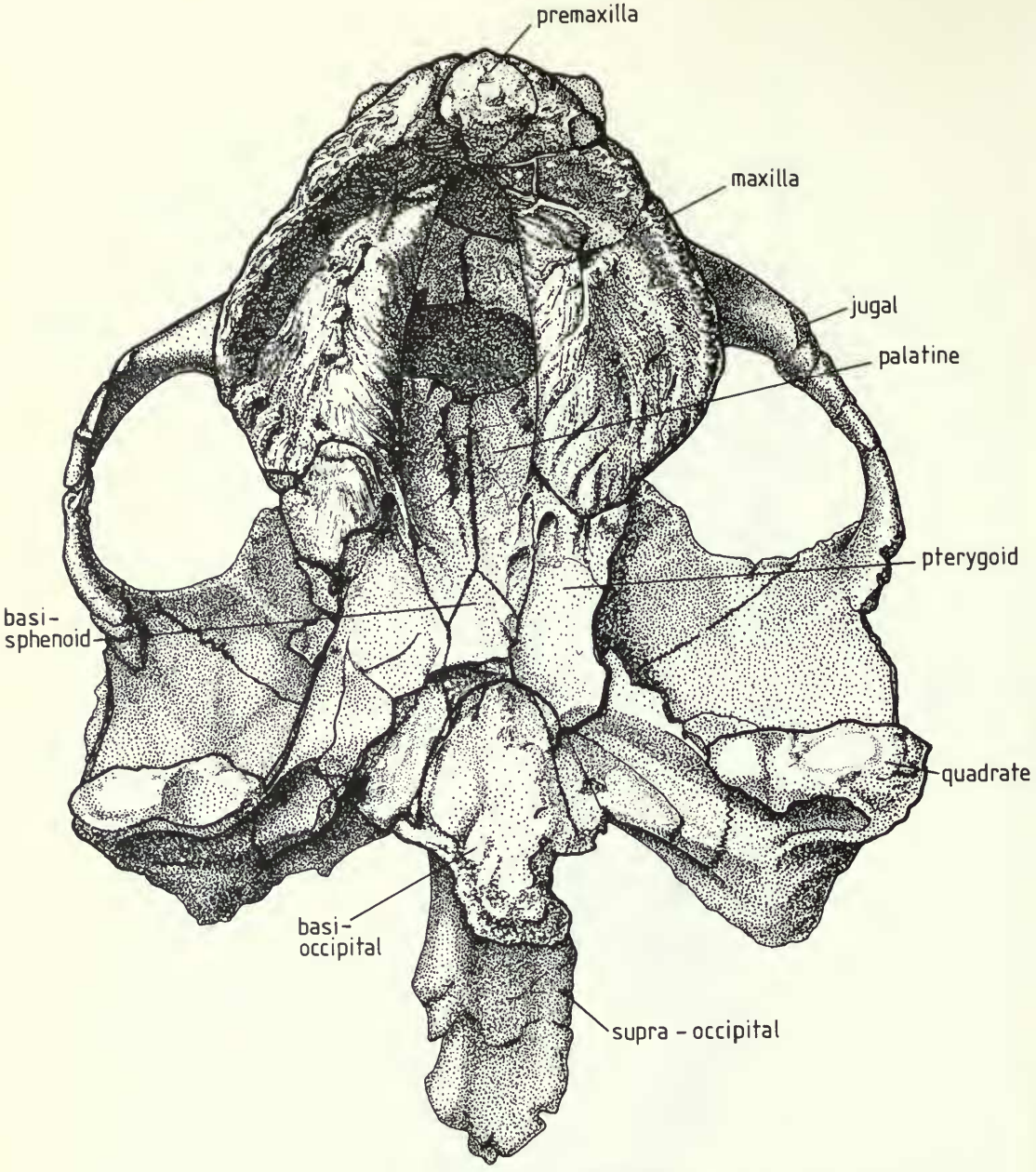

Fig. 5 *Eurycephalochelys fowleri* Moody & Walker, R8694. Palatal view of skull, × 0·75.

In occipital view there is a well-developed depression on either side of the foramen magnum. Each is centred on the posterior edge of the exoccipital and to a lesser extent the opisthotic. This region is rather variable in trionychids, but no modern form appears to have developed such a depression in which the opisthotic overhangs the dorsal surface. In fact in *Cycloderma* and *Chitra* there is no comparable feature and in the other trionychids it is represented by a shelf which can be clearly seen in dorsal view. The fenestra postotica is unrestricted, with no indication of an ascending process on the pterygoid. This is at variance

with the holotype, but Loveridge & Williams (1954) show that this could be a variable character, at least within *Trionyx*.

MEASUREMENTS (in millimetres)

(E = estimated)	R8694	R8695	R8445 (Holotype)
Actual length premaxilla – occipital condyle	167	234 (E)	157
Maximum length premaxilla – supra-occipital spine	212	–	215 (E)
Width across quadrates	147	207	132
Width across external nares	34	42	23
Anterior margin of orbit to premaxilla	50	–	42
Minimum depth of maxilla below orbit	31·5	42 (E)	30
Maximum length of orbit	24	–	26
Maximum depth of orbit	22	–	22
Estimated length of anterior palatine foramen	16	–	8
Estimated length of intermaxillary suture	19	–	13
Estimated length of choanae	20	–	17
Maximum width across maxilla in palatal view	89	116 (E)	87
Maximum width of articular surface of quadrate	34·5	52	29
Maximum width across jugals	144	–	–
Minimum width of interobital bar	22	–	–
Tip of premaxilla to maximum width of maxilla	47	55	43
Maximum width across orbits	59	70 (E)	54
Minimum width across pterygoids	58 (E)	78	54 (E)

COMPARISONS. There can be little doubt that *Eurycephalochelys* more closely resembles *Trionyx* than any other fossil or Recent trionychid. It does, however, bear comparison with both *Cyclanorbis* and *Cycloderma*. For whereas the shape of the external nares is broader than high the reverse condition is accepted as normal for *Trionyx*. In palatal view the intermaxillary foramen is of moderate size, approximating to the length of the intermaxillary suture. This condition is similar to that of *Trionyx, Cycloderma* and *Lissemys*, but differs from that in *Cyclanorbis* and *Chitra* where the foramen is either highly reduced or even absent. The vomer, although missing, was probably not as well developed as that of *Trionyx* or *Chitra*, and there is no indication of any marked vomerial ridge on the roof of the choanal vault region. *Cyclanorbis, Lissemys* and to a lesser extent *Cycloderma* exhibit a weak vomerial ridge. The posterior openings of the foramen posterior canalis carotici interni cannot be seen in palatal view, and in this respect *Eurycephalochelys* resembles *Chitra* and no other trionychid. In occipital view it bears a distinct resemblance to *Trionyx*, but the depressions for the attachment of the cervical musculature on either side of the foramen magnum are rather better developed than in other trionychids. The closest comparison to this condition has been observed in certain specimens of *T. cartilagineus* (Boddaert) but even in this species it is not so pronounced as in *Eurycephalochelys*. The fenestra postotica is not restricted in R8694, and although this contrasts with the limited development of the ascending process of the pterygoid in the holotype, Loveridge & Williams (1957) have noted that specimens referred to *T. triunguis* (Forskål) exhibit similar intraspecific variation. Within the orbit, the position of the canalis alveolaris superior (internal maxillary foramen) is more laterally placed than in other trionychids. This feature appears to be somewhat variable, however, for in the holotype this foramen is situated in the medial wall of the maxilla. Further, the anterior opening of the foramen palatinum runs to the external side of the ascending process of the palatine, as in *Trionyx* and *Cycloderma*, whereas in *Cyclanorbis* and *Lissemys* it exits through the centre of that bone. The structure of the quadrate remains enigmatic, for the stapedial foramen lies behind that of the holotype; in fact it is only slightly more forward than in any trionychid other than *Chitra*. Although some crushing has affected both the holotype and R8694 it is thought that the variation in this character is intraspecific rather than preservational.

Conclusions

Since the original description of *Eurycephalochelys fowleri*, a major work on the testudinates of the Cretaceous and Tertiary deposits of France has been presented by de Broin (1977). In this paper the author makes comparisons between the various fossil trionychids of Belgium, France and England, and attempts in several places to link the European genera and species with those of the rest of the world. In dealing with fragmentary material from the Palaeocene and Lower Eocene deposits of the Paris Basin, she associates the European species *Trionyx vittatus* Pomel (1847) with the North American genus *Palaeotrionyx* Schmidt (1945). Her arguments for this association are based essentially upon shell ornament, the same reasoning leading her to refer *T. levalensis* Dollo to the same genus.

De Broin (1977) has followed us (Moody & Walker 1970) in regarding *T. levalensis* as a nomen nudum, but disagrees with us in inferring that *T. levalensis* and *E. fowleri* are conspecific. We believe this is incorrect, for whilst we appreciate that a case may exist for the association of fragmentary postcranial material on shell ornament alone, we find the case for association based upon poorly preserved skull fragments unacceptable, particularly when de Broin (1977: 151) claims that the cranial material from Leval is insufficient for determination. The lower jaw she refers (1977: pl. 8, figs 3–4) to *Palaeotrionyx vittatus* (Pomel) is in itself indeterminate: the fragment is associated with *Eurycephalochelys* and *T. levalensis* purely on size, which although convenient lacks justification. De Broin is correct in her assumption that a number of large trionychids were present in the Lower Eocene, with large skull and postcranial material recorded from both Europe and North America. It is likely, however, that the erection of a new subfamily may prove more acceptable than the reference of all known material to the 'comprehensive genus' *Palaeotrionyx*. A similar argument to that for *Eurycephalochelys* may also be put on behalf of *Conchochelys admirabilis* Hay (1905); from the original figures this bears little resemblance, except for size, to *Palaeotrionyx, sensu* de Broin.

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